FLORAL NECTARIES IN MELASTOMATACEAE AND THEIR SYSTEMATIC AND EVOLUTIONARY IMPLICATIONS[1]

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ABSTRACT

The vast majority of the 4,500–5,000 species in the primarily tropical family Melastomataceae do not produce floral nectar, instead relying on pollen as the pollinator reward. To determine the anatomical basis for nectar production in the relatively few nectar-producing taxa, we examined 40 species in 17 genera representing known nectar producers and genera and species not reported to secrete nectar. Our anatomical investigations included six species in three genera of Memecylaceae, a family traditionally placed within Melastomataceae. We also conducted field observations to clarify the site of nectar secretion in several genera. No structural nectaries (derived from differentiated parenchyma) were detected in any of the species examined. Rather, most nectar-secreting species appear to produce the nectar from a thickened staminal vascular bundle. Within the order Myrtales, this type of nonstructural androecial nectary is limited to Melastomataceae and is apparently very rare among angiosperms as a whole. Two additional methods of nectar production in Melastomataceae were revealed: secretion from the petal tips in *Medinilla*, and, although field confirmation is still required, from the stigma in *Miconia*. Given the ancestral myrtalean nectary type, it seems clear that structural nectaries were lost in the evolutionary lineage ancestral to Melastomataceae and Memecylaceae. In most nectar-producing Melastomataceae the re-evolution of nectaries appears to be related to a shift in pollinator interactions, specifically from vibratile-pollination bees at lower elevations to vertebrates at higher elevation. We consider the independent development of nectaries in several lineages of Melastomataceae to be the most parsimonious explanation for the diversity of nectary types within the family and for the scattered phylogenetic positions of nectar-producing taxa.

The family Melastomataceae, with ca. 200 genera and 4,500–5,000 species, is the largest in the order Myrtales. This primarily tropical family is distributed worldwide but particularly well represented in tropical and subtropical areas of the New World. Most members of the family produce no floral nectar, relying instead on pollen as the principal pollinator reward (for review see Renner, this volume). Species in at least two genera, *Tibouchina* (= *Purpurella*) (Ule, 1896) and *Brachyotum* (Lagerheim, 1899), however, have long been known to produce nectar. Additional observations of nectar production, or presumed production, have been made more recently on these and several other melastome genera, including *Blakea* (Lumer, 1980; Lumer & Schoer, 1986), *Huilaea* (Snow & Snow, 1980), and *Miconia* (Mori & Pipoly, 1984). Most reports that note the location of nectar secretion within the flower generally found the nectar to emanate from the stamens. This strongly contrasts with the situation in most myrtalean families in which floral nectaries are located either on the floral tube, the gynoecium, or at the floral tube–gynoecium junction.

Floral nectaries of Melastomataceae have been little studied, and nothing has been reported pre-

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viously about their anatomical structure. The primary purpose of this study is to elucidate the structure of Melastomataceae nectaries through anatomical examination and to confirm the unusual location of nectar secretion through field observations. Our investigation of floral nectary structure extends to representative genera of Memecylaceae, a family traditionally included in Melastomataceae as a tribe or subfamily. The anther connective of Memecylaceae contains a distinctive depressed gland structure that had previously been described as a nectary (Burck, 1891; Subramanyam, 1949). In *Mouriri*, however, these glands have recently been found to secrete a lipid-rich substance, suggesting that they are elaiophores (Buchmann & Buchmann, 1981).

Materials and Methods

We examined anatomically flowers of 40 species in 17 genera of Melastomataceae, representing known nectar producers and genera and species not reported to secrete nectar. In addition, six species of Memecylaceae in three genera were investigated. FAA-fixed collections were made by the authors and by numerous collaborators worldwide (Table 1).

After dehydration through a t-butyl alcohol series and embedding in Paraplast with MP 57–58 C°, flowers (and sometimes stamens alone) were sectioned transversely and longitudinally at 8–10 μm thickness; the sections were stained with hematoxylin, safranin, and fastgreen FCF and were mounted with Entellan. Dark staining by hematoxylin represents a concentration of cytoplasm in cells, indicating high metabolic activity such as seen in active nectaries. In other families of the Myrtales, this staining method has fully demonstrated the location and size of nectariferous tissue (Tobe, pers. obs.); if present, nectaries are thus easily distinguished from other tissue by their dense staining.

We noticed that certain species, particularly those known to secrete nectar, have a conspicuously thickened staminal vascular bundle. Thus, for comparative purposes, the thickness of the staminal vascular bundle is presented as a relative value (Table 1). The "relative thickness" of stamen vascular bundles is calculated as: radial thickness of the vascular bundle (t)/radial thickness of the filament (T). Calculations were made on the basis of two or three stamens. Relative thickness values are presented as a range, since the thickness of the filament and the vascular bundle can differ at varying points along the same filament.

Field observations of nectar secretion in *Brachyotum*, *Chalybea*, and *Tibouchina* were conducted while field collecting floral material for this study. Fresh flowers were examined for evidence of nectar, and the location of nectar secretion within the flower was noted. Nectar quantity and sugar concentration were measured using microcapillary tubes and a Reichert temperature-compensated hand refractometer (model 10431). Nectar sugar concentration measurements (% brix) were subsequently converted to sucrose-equivalents (weight by total weight).

Results

We did not detect densely staining structural nectaries in the flowers of any of the species examined of Melastomataceae and Memecylaceae. Three significant features were noted, however. First, stamens of some melastomes, particularly those known to secrete nectar, have a markedly thickened vascular bundle in relation to the filament or anther connective. Relative thickness of staminal vascular bundles of nectar-producing and non-nectar-producing species are presented in Table 1. The relative thickness values of staminal vascular bundles in nectar-producers normally exceed 0.3 (mean 0.34), whereas most other melastomes examined range between 0.1 and 0.3 (mean 0.23), a statistically significant difference ($P < 0.001$). Second, although no densely staining structural nectaries were found, many of these thickened vascular bundles showed relatively dark-staining phloem cells, indicating that they are cytoplasm rich and may be fulfilling a nectary function. Third, many of the nectar-secreting species have external slits that develop on or near the geniculum of the filament and that may represent a nectar emission pathway.

Information on the site of nectar secretion and on known or putative pollination vectors for nectar-producing Melastomataceae is summarized in Table 2. Examined genera that are known or strongly suspected to produce nectar are discussed individually below. Members of several other genera may also secrete nectar but were not examined. These include two additional Andean genera that hummingbirds have recently been observed visiting, *Centronia excelsa* (Bonpl.) DC. (Neill, pers. comm., 1987) and *Meriania tomentosa* (Cogn.) Wurdack (van der Werff, pers. comm., 1987).

MELASTOMATACEAE

Blakea. Three species of *Blakea* were examined anatomically, with *B. chlorantha* Almeda known

TABLE 1. Species examined anatomically. Relative thickness of staminal vascular bundles given at right. Tribal positions of genera essentially follow Cogniaux (1891) and van Vliet et al. (1981).

Species	Collection Voucher	Relative Thickness of Staminal Bundle, t/T (see Figs. 5 and 10)
Melastomataceae		
Tribe Microlicieae		
Rhynchanthera paludicola (J. D. Smith) Gleason	Costa Rica, *Grayum et al. 6009* (MO)	0.24–0.26
Tribe Tibouchineae		
Brachyotum campanulare (Bonpl.) Triana	Ecuador, *Stein & D'Alessandro 2709* (MO)	0.32–0.40
B. ledifolium (Desr.) Triana	Ecuador, *Stein et al. 2701* (MO)	0.39–0.45
B. ledifolium (Desr.) Triana	Ecuador, *Stein 2892* (MO)	0.32–0.37
B. lindenii Cogn.	Ecuador, *Stein 2890* (MO)	0.33–0.34
B. microdon (Naud.) Triana	Bolivia, *Solomon 13089* (MO)	0.33–0.36
B. sanguinolentum (Naud.) Triana	Bolivia, *Solomon 13859* (MO)	0.32–0.33
Heterocentron elegans (Schlecht.) Kuntze	Cultivated, Royal Botanic Gardens, Sydney, *Griggs 7145* (NSW)	0.16–0.23
Tibouchina bicolor (Naud.) Cogn.	Bolivia, *Solomon 13862* (MO)	0.30–0.36
T. clavata (Pers.) Wurdack	Cultivated, Mathias Botanical Garden, *Prigge 6525* (UCLA)	0.29–0.31
T. grossa (L.f.) Cogn.	Colombia, *Stein & McDade 3147* (MO)	0.38–0.41
T. heteromalla Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6445* (UCLA)	0.19–0.24
T. laxa Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6211* (UCLA)	0.32–0.33
T. multiflora Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6524* (UCLA)	0.24–0.28
T. semidecandra (DC.) Cogn.	Cultivated, Missouri Botanical Graden, *Tobe s.n.* (no voucher)	0.34–0.37
T. stenocarpa (DC.) Cogn. var. *boliviensis* Cogn.	Bolivia, *Solomon 13231* (MO)	0.32–0.35
T. urvilleana (DC.) Cogn.	Cultivated, Mathias Botanical Garden, *Prigge 6444* (UCLA)	0.32–0.34
Tribe Rhexieae		
Monochaetum floribundum (Schlecht.) Naud.	Mexico, *Breedlove & Almeda 56716* (CAS)	0.27–0.33
Tribe Sonerileae		
Sonerila picta Korth.	Thailand, *Maxwell s.n.* (PDA)	0.23–0.27
Sonerila sp.	Sri Lanka, *Jayasuriya 3009* (PDA)	0.22–0.25
Sonerila sp.	Sri Lanka, *Jayasuriya 3030* (PDA)	0.26–0.27
Sonerila sp.	Sri Lanka, *Jayasuriya 3094* (PDA)	0.24–0.25
Tribe Bertolonieae		
Bertolonia maculata DC.	Cultivated, Missouri Botanical Garden, *Zardini s.n.* (no voucher)	0.23–0.24
Monolena multiflora Warner ined.	Panama, *Churchill 4155* (MO)	0.17–0.23
Triolena hirsuta (Benth.) Triana	Costa Rica, *Schatz 999* (WIS)	0.17–0.20
Tribe Dissochaeteae		
Medinilla fuchsioides Gardn.	Sri Lanka, *Jayasuriya 3351* (PDA)	0.23–0.24
M. myriantha Merr.	Cultivated, Mathias Botanical Garden #78-069 (no voucher)	0.10–0.13
Tribe Miconieae		
Bellucia pentamera Naud.	Costa Rica, *Hammel et al. 14149* (MO)	0.08–0.10
Chalybea corymbifera Naud.	Colombia, *Stein et al. 3610* (MO)	0.26–0.33
Miconia dodecandra (Desr.) Cogn.	Mexico, *Breedlove & Almeda 57466* (CAS)	0.14–0.22

TABLE 1. Continued.

Species	Collection Voucher	Relative Thickness of Staminal Bundle, t/T (see Figs. 5 and 10)
M. melanotricha (Triana) Gleason	Panama, *McPherson 8060* (MO)	0.13–0.22
M. minutiflora (Bonpl.) DC.	Venezuela, *Berry 4417* (VEN)	0.26–0.29
M. reducens Triana	Panama, *Sytsma 4032* (MO)	0.18–0.19
Tribe Blakeeae		
Blakea chlorantha Almeda	Costa Rica, *Haber 1197* (MO)	0.21–0.27
B. foliacea Gleason	Panama, *Churchill 5463* (MO)	0.21–0.25
B. sp. nov.	Costa Rica, *Grayum et al. 3553* (MO)	0.18–0.23
Topobea pittieri Cogn.	Panama, *Churchill 5477* (MO)	0.11–0.13
Tribe Astronieae		
Astronia candolleana Cogn.	Philippines, *Hernaez 3829* (CAHP)	0.19–0.23
A. ferruginea Elmer	Taiwan, *Peng 5247, 5503* (HAST)	0.21–0.29
A. meyeri Merr.	Philippines, *Hernaez 3832* (CAHP)	0.17–0.20
Memecylaceae		
Tribe Memecyleae		
Memecylon cantleyi Ridley	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.23–0.25
M. caeruleum Jack.	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.15–0.23
Mouriri myrtilloides (Sw.) Poir.	Panama, *Hamilton 2883* (MO)	0.20–0.25
M. nervosa Pilger	Brazil, *Renner 249* (US)	0.16–0.18
Tribe Pternandreae		
Pternandra caerulescens Jack.	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.23–0.24
P. echinata Jack.	Cultivated, Singapore Botanical Garden, *Maxwell s.n.* (no voucher)	0.17–0.24

to produce nectar. Two additional nectar-producing species have recently been reported, *B. austin-smithii* Standl. and *B. penduliflora* Almeda (Lumer & Schoer, 1986). There is some disagreement concerning the site from which nectar is secreted in this genus. Lumer (1980, and pers. comm., 1985) stated that in *B. chlorantha* nectar appears to be secreted in the area at the base of the stamens, either at the junction of the filament and floral tube or at the base of the filaments. According to Haber (pers. comm., 1985), however, nectar is secreted on the abaxial surface of the filaments (the side facing the corolla wall), with the nectar forming thick droplets between the filament and the corolla.

Anatomical sections of *Blakea chlorantha* flowers do not show a densely staining nectary anywhere on the floral tube wall (Fig. 1), nor do stamens have an externally or internally differentiated nectariferous structure (Figs. 2, 3). Stamens are folded inward in bud, with a geniculum present just above the midpoint. Slitlike structures are present on the adaxial surface of the geniculum (arrows in Figs. 1–3). The relative thickness value of the vascular bundles is fairly low (0.21–0.27) compared with other nectar producers (Fig. 5). These vascular bundles, however, are relatively densely staining, particularly in the upper part of the filament and at the connective (Figs. 3–5). A major part of the staminal vascular bundle appears to consist of small, cytoplasm-rich phloem cells. Parenchyma cells surrounding the staminal vascular bundle are not specialized (Figs. 4, 5), suggesting that they are not nectariferous.

Stamens of *Blakea* sp. nov. (fide F. Almeda) and *B. foliacea* are folded inward in bud at the anther–filament junction, and filament slits are not present. Although, like *Blakea chlorantha*, they have a thin more or less densely staining vascular bundle, they differ in that the staminal vascular bundle is surrounded by a thick-walled tanniferous epidermis and by some underlying tanniferous cell layers. *Blakea* sp. nov. and *B. foliacea* stamens are unlikely to secrete nectar through such tanniferous tissue, and nectar production has never been reported in either of these two species.

Brachyotum. All *Brachyotum* species investigated in the field were found to produce nectar,

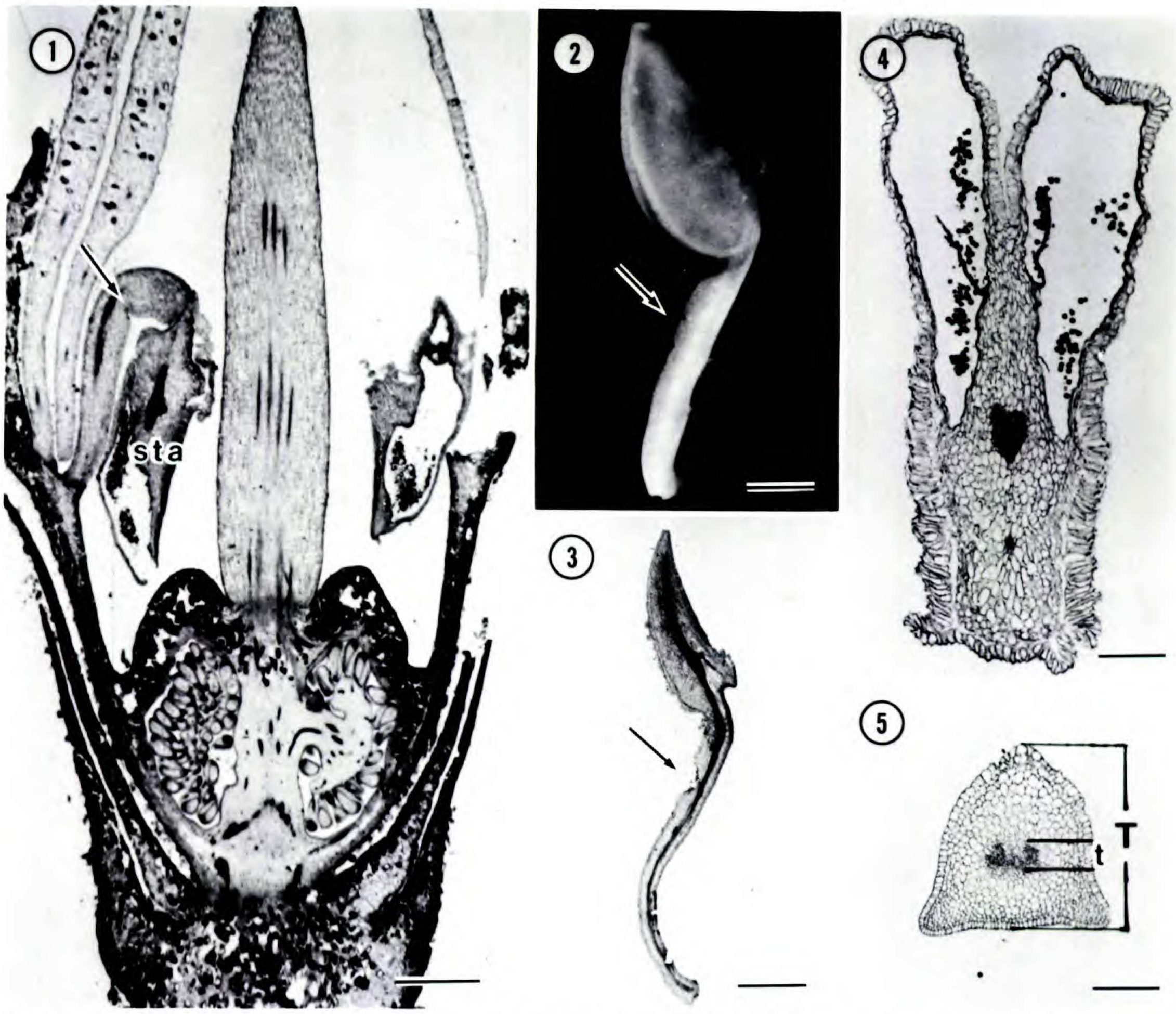
TABLE 2. Summary of data on nectar secretion and pollinators in nectar-producing Melastomataceae.

Species	Nectar Secretion Site	Time of Secretion	Pollinators	References
Blakea austin-smithii Standl.	Base of filaments	Nocturnal	Rodents	Lumer & Schoer, 1986
B. chlorantha Almeda	Abaxial surface or base of filaments	Nocturnal	Rodents	Lumer, 1980
B. penduliflora Almeda	Base of filaments	Nocturnal	Rodents	Lumer & Schoer, 1986
Brachyotum ledifolium (Desr.) Triana and other *Brachyotum* species	Adaxial surface of filaments	Diurnal	Hummingbirds	Lagerheim, 1899; Stein, pers. obs.
Chalybea corymbifera Naud.	Base of stamens? (see text)	Diurnal	Hummingbirds?	Stein, pers. obs.
Huilaea macrocarpa Uribe	Not known	Diurnal	Hummingbirds	Snow & Snow, 1980
Medinilla magnifica Lindl.	Tips of petals	Diurnal	Not known	Tobe et al., in prep.
Miconia minutiflora (Bonpl.) DC.	Not known (stigma?)	Morning	Bees	Mori & Pipoly, 1984
Tibouchina cleistoflora Ule	Adaxial surface of filaments	Not known	Bees	Ule, 1896; Renner, this volume
T. grossa (L.f.) Cogn.	Adaxial surface of filaments	Nocturnal/ Diurnal	Bats and hummingbirds	Vogel, 1957; Stein, pers. obs.
T. hospita (DC.) Cogn.	Adaxial surface of filaments	Not known	Bees	Ule, 1896; Renner, this volume
T. itatiaiae (Wawra) Cogn.	Adaxial surface of filaments	Not known	Not known	Ule, 1896

confirming previous reports (Lagerheim, 1899; Vogel, 1957; Wurdack, 1965), and it is likely that this entire Andean genus is nectariferous. From field observations, the nectar appears to be secreted by the filament at the slitlike structure located on or just below the geniculum on the adaxial filament face (Fig. 6) and forms large droplets suspended between adjacent pairs of filaments. Nectar concentration ranged from a high of 20–22% sucrose-equivalents in *B. ledifolium* (Desr.) Triana to a low of 15–16.5% in *B. campanulare* (Bonpl.) Triana, values consistent with most hummingbird-pollinated flowers (Baker, 1975).

Anatomical sections of stamens do not show any differentiated nectariferous structure in the filaments. Stamens of *Brachyotum ledifolium* have a thick vascular bundle running the length of the filament (Fig. 7) to the connective (Fig. 8). The staminal vascular bundle is densely staining and contrasts with the surrounding nonspecialized parenchyma cells. All other examined species of *Brachyotum* contain a similar thick, densely staining staminal vascular bundle: *B. campanulare* (Fig. 10), *B. lindenii* Cogn., *B. microdon* (Naud.) Triana, and *B. sanguinolentum* (Naud.) Triana (Fig. 9). This similarity in staminal anatomy suggests that all these species exude nectar from the filament.

Chalybea. *Chalybea* is a monotypic genus of the Colombian Andes closely related to, if not congeneric with, the nectar-producing genus *Huilaea*. Poorly known and consisting only of *C. corymbifera* Naud. (= *Pachyanthus corymbiferus* [Naud.] Cogn.), *Chalybea* recently has been resurrected on the basis of material newly collected for this study (Wurdack, 1988). We have observed nectar secretion from *C. corymbifera* and measured the nectar sugar concentration at 16.5% sucrose-equivalents. Pinpointing the site of secretion is problematic. Nectar was collected from the summit of the inferior ovary; however, the nectar was observed and measured several hours after the normally pendulous flowers were collected and could have migrated to this location. Stamens are bent inward in bud and have neither a pronounced geniculum nor filament slits (Figs. 11, 12). Anatomical sections do not show a differentiated nectariferous structure at the ovary summit (Fig. 11). While stamens do not have either externally differentiated structures or densely staining nectariferous tissue (Figs. 11, 12), they do contain a thick vascular bundle running through the filament (Fig. 14) to the connective (Fig. 13), suggesting staminal secretion. Tanniferous parenchyma cells surrounding the staminal vascular bundle appear unfavorable



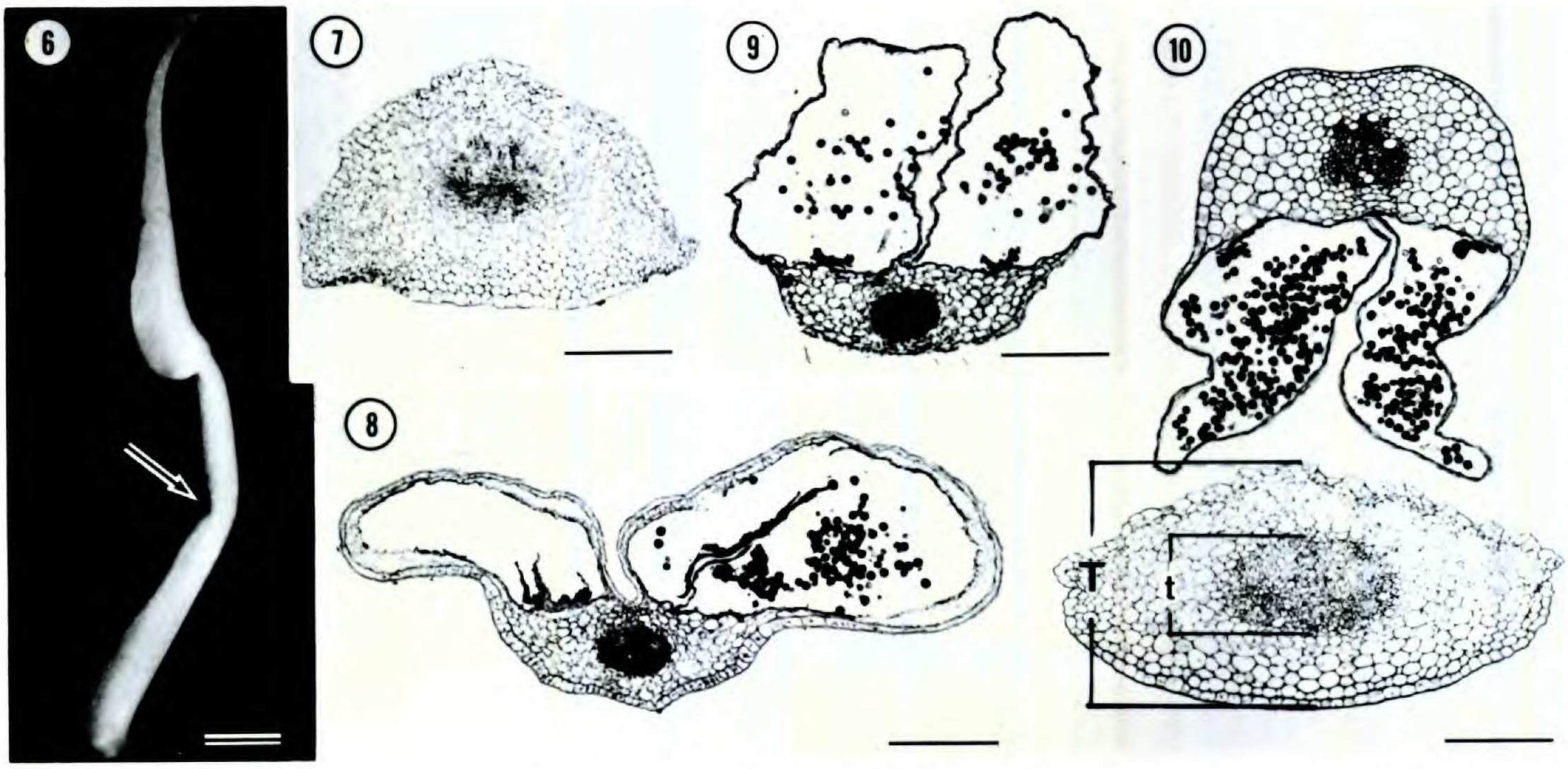
FIGURES 1–5. *Blakea chlorantha*.—1. Longitudinal section (LS) of flower.—2. Stamen.—3. LS of stamen.—4,5. Transverse sections (TS) of anther and of filament. Arrows in Figures 1–3 indicate a depression or break formed at the inner side of the bend. Abbreviation: sta, stamen. T and t in Figure 5 are thickness of filament and of vascular bundle respectively, which are measured for calculation of relative thickness of staminal vascular bundles (see text for explanation). Scale bars = 1 mm in Figures 1–3; 0.2 mm in Figures 4, 5.

for secretion of nectar. These tanniferous cells, however, are much less conspicuous in the lower part of the filament, and nectar thus may exude from the filament in this location, perhaps accounting for its observed presence on the ovary summit.

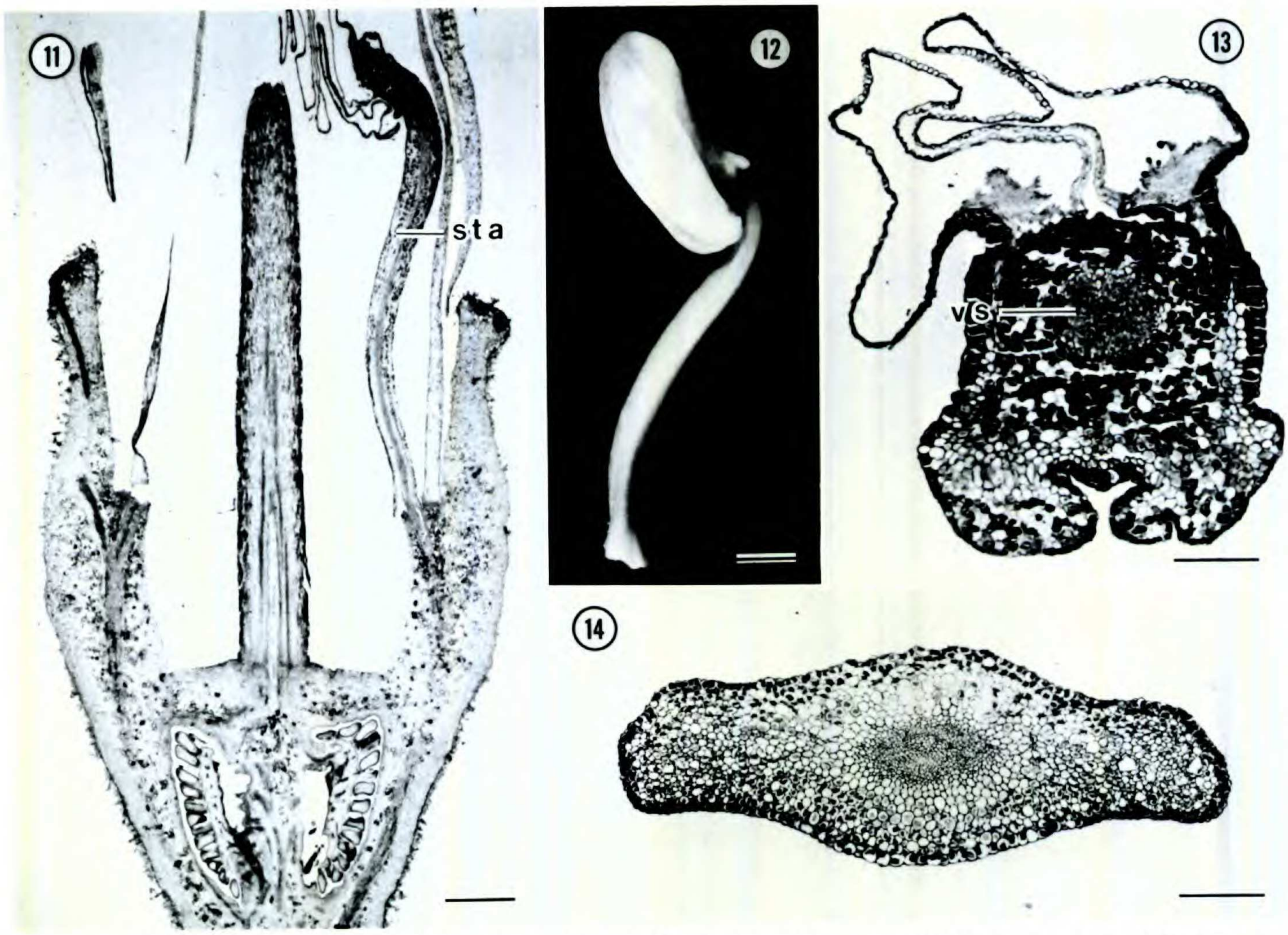
Huilaea. Snow & Snow (1980) reported nectar production by *Huilaea macrocarpa* Uribe and measured the nectar sugar concentration to range from 12 to 16% with a mean of 13.4%. No information was provided as to the precise location of nectar secretion in these pendulous flowers.

Tibouchina. Nine species of *Tibouchina* were examined, including the Andean *T. grossa*, which is known to produce nectar. Brazilian *Tibouchina* species reported to secrete nectar include *T. cleistoflora* Ule, *T. hospita* (DC.) Cogn., and *T. itatiaiae* (Wawra) Cogn. (Ule, 1896). Our observations of nectar secretion in *T. grossa* differ somewhat from those of Vogel (1957), who considered the nectar to exude from the inner wall of the floral tube below the insertion of the stamens. *Tibouchina grossa* flowers are open-campanulate and oriented horizontally with all stamens arranged in a half-circle in the lower side of the corolla. We observed nectar droplets forming on the adaxial surfaces of the filaments near the geniculum. The drops are at first suspended between adjacent filaments and occasionally between the filaments and style. The rather copious nectar then flows down the filaments to collect either in the floral tube or on the convex lower petals. We measured sugar concentration of *T. grossa* nectar at 14.5% sucrose-equivalents.

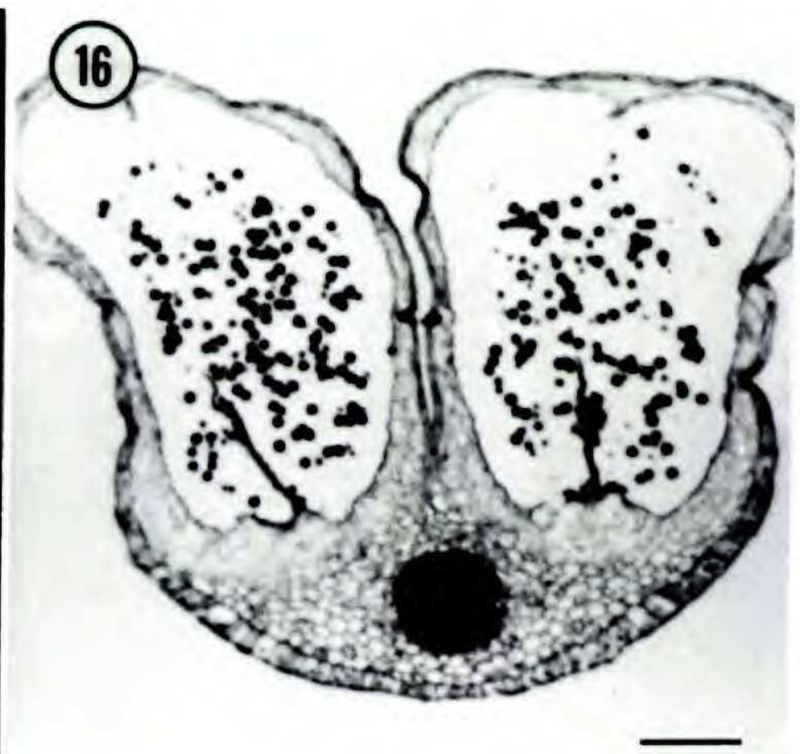
No densely staining differentiated structure was found in the filaments of *Tibouchina grossa* (Fig.

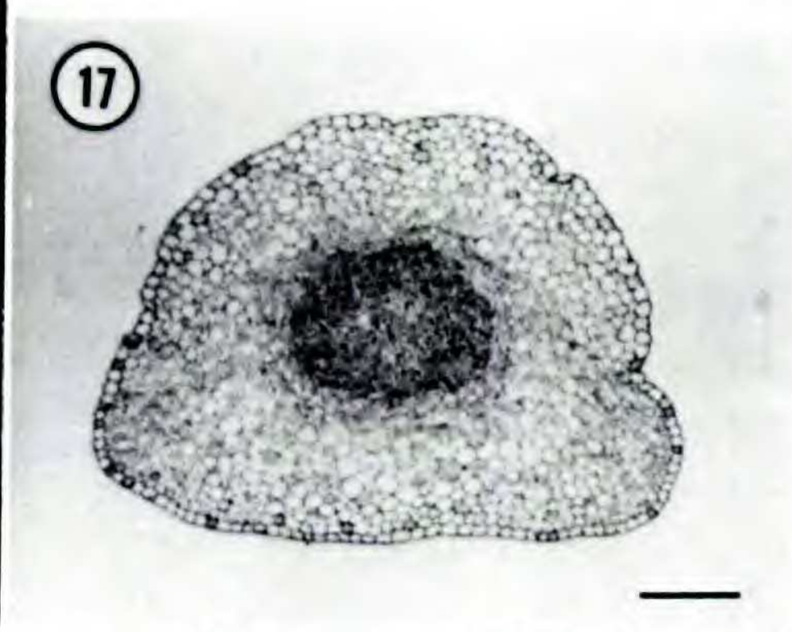


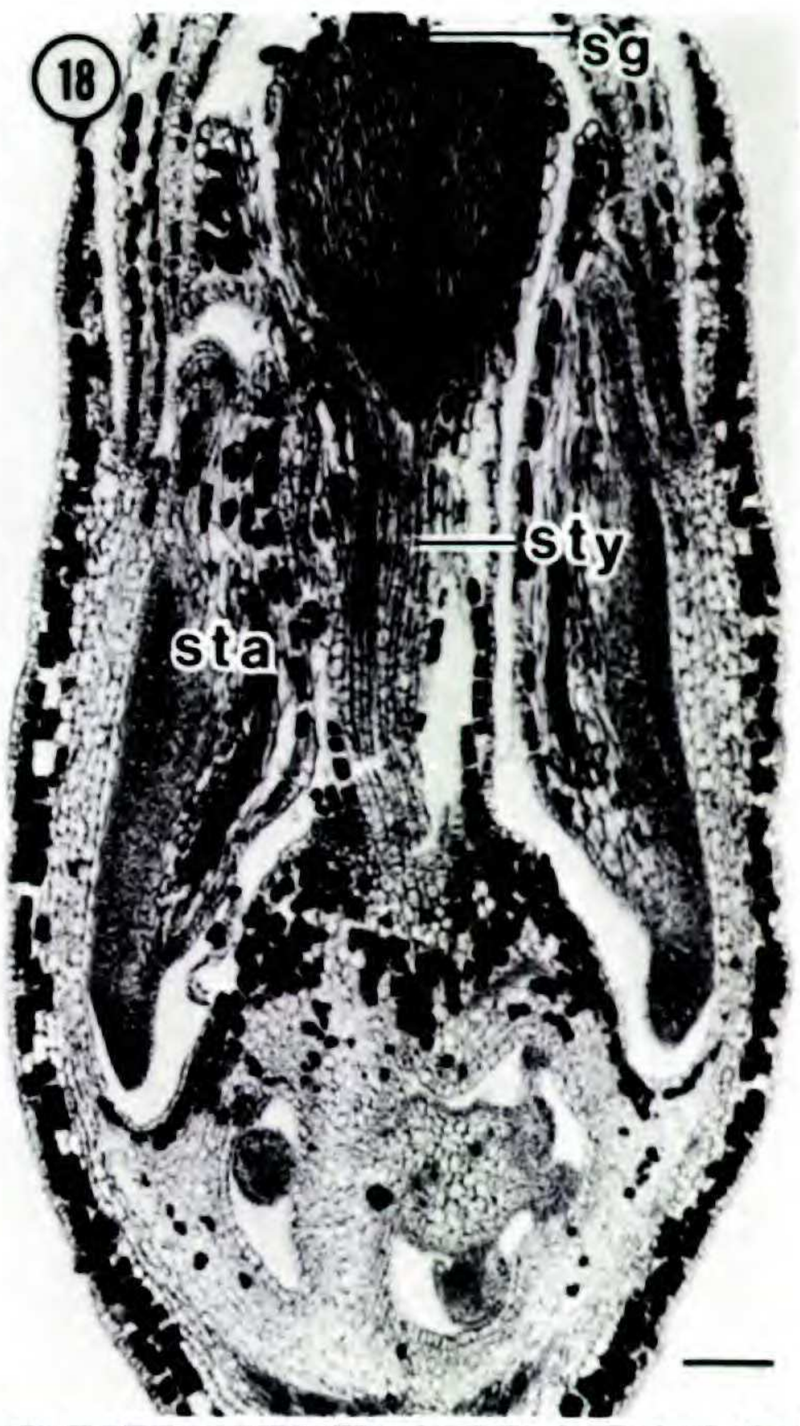
FIGURES 6–10. *Brachyotum.*—6. Stamen of *Brachyotum ledifolium.*—7, 8. Transverse sections (TS) of filament and of anther of *Brachyotum ledifolium.*—9. TS of anther of *Brachyotum sanguinolentum.*—10. TS of anther (above) and of filament (below) (the adaxial sides of which are opposite) of *Brachyotum campanulare.* Note thick staminal vascular bundles in all species. Abbreviations (T and t) in Figure 10 correspond to those in Figure 5. Scale bars = 1 mm in Figure 6; 0.2 mm in Figures 7–10.

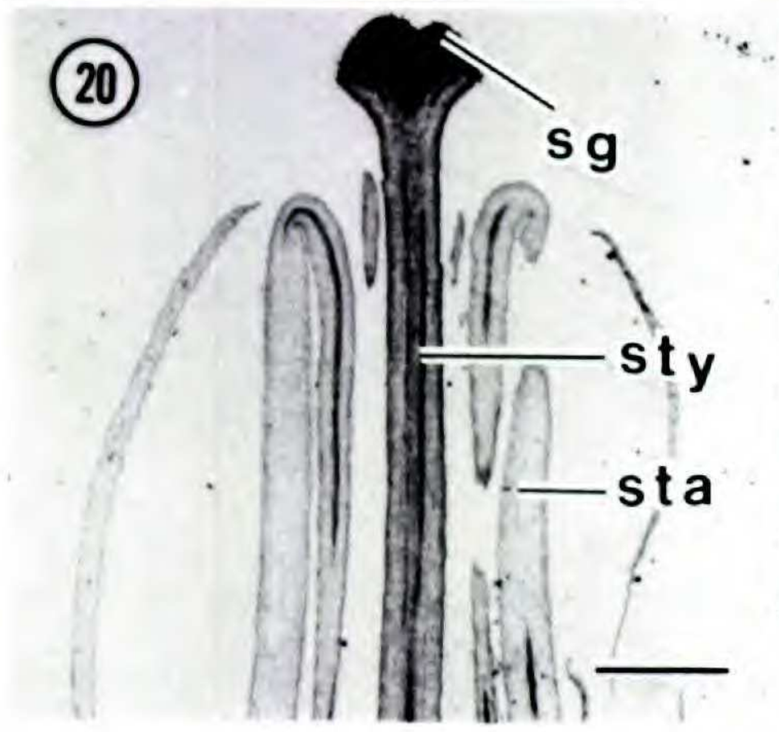


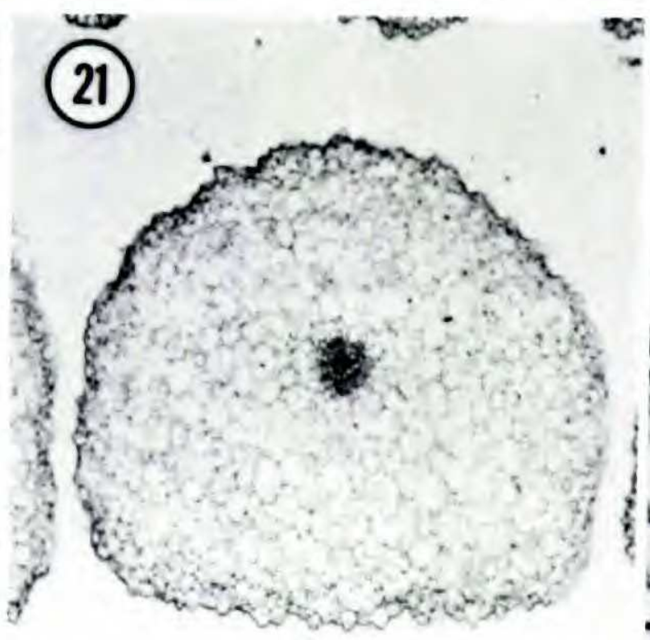
FIGURES 11–14. *Chalybea corymbifera.*—11. Longitudinal section of flower.—12. Stamen.—13, 14. Transverse sections of anther and of filament. Abbreviations: sta, stamen; vs, vascular bundle. Scale bars = 1 mm in Figures 11, 12; 0.2 mm in Figures 13, 14.

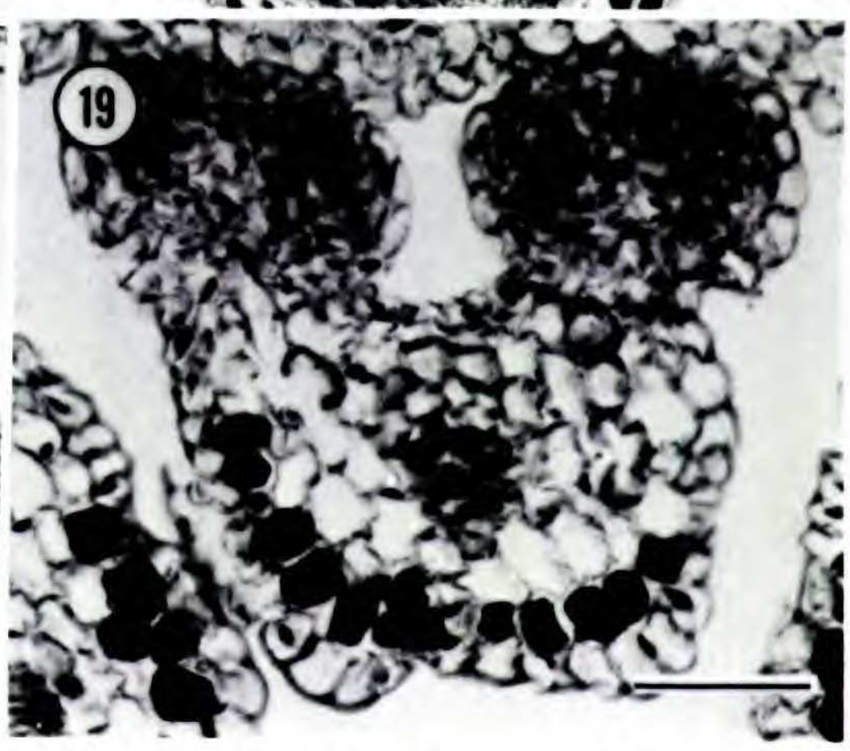












FIGURES 15–21. *Tibouchina* and *Miconia*. —15. Stamen of *Tibouchina grossa*, which is bent at a hinge. —16, 17. Transverse sections (TS) of anther and of filament of *Tibouchina grossa*, showing thick vascular bundle. —18. Longitudinal section (LS) of flower bud of *Miconia minutiflora*. —19. TS of young anther of *Miconia minutiflora*. —20. Upper half of LS of flower bud of *Miconia melanotricha*. —21. TS of filament of *Miconia melanotricha*. Abbreviations: sg, stigma; sta, stamen; sty, style. Scale bars = 1 mm in Figures 15, 20; 0.2 mm in Figures 16, 17, 18, and 21; 0.05 mm in Figure 19.

15). Instead, stamens of *T. grossa* have a thick, densely staining vascular bundle surrounded by nonspecialized parenchyma cells (Figs. 16, 17). Relatively thick staminal vascular bundles are observed in all *Tibouchina* species investigated (see Table 1), although nectar production has so far not been reported in those other species.

Medinilla. The Old World genus *Medinilla* includes certain species that morphologically appear to be good candidates for bird pollination. We examined anatomically one such species, *Medinilla fuchsioides* Gardn., but found the staminal vasculature to be unexceptional. Subsequent to this, however, we found cultivated material of *M. magnifica* Lindl. at the Berlin Botanical Garden to secrete nectar from the petal tips. Anatomical investigations of this very unique nectar secretion method are currently under way (Tobe et al., in prep).

Miconia. In discussing a mass flowering episode of *Miconia minutiflora* (Bonpl.) DC, Mori & Pipoly (1984) reported the presence of nectar as a pollinator reward in this species. In other localities, however, this lowland species has not been found to secrete nectar (Renner, 1983).

Only young buds of *Miconia minutiflora* were

available for the present study. Anatomical sections of this material indicate no structure likely to produce nectar in either the stamens or around the floral tube–gynoecium junction (Fig. 18). Flowers are very small, with the filaments supplied by a relatively thin vascular bundle (Fig. 19). Anatomical sections show, however, that *M. minutiflora* has a remarkably conspicuous stigma supplied by ample, densely staining vascular tissue (Fig. 18).

Hummingbirds have been observed visiting *Miconia melanotricha* (Triana) Gleason (Almeda, pers. comm., 1986), and this species may produce nectar. The flowers appear morphologically well suited for hummingbird pollination, given their large size (10–15 mm in diameter and 23–25 mm long) and red petals. This species also has longitudinally dehiscent anthers rather than the apically poricidal anthers typical of bee-pollinated melastomes. Anatomical sections do not show densely staining structures or tissue, and the stamens have a thin vascular bundle (Fig. 21). As in *M. minutiflora*, however, the stigma and supporting vascular tissue are unusually densely staining (Fig. 20).

Miconia robinsoniana Cogn. was reported to produce nectar in a survey of the foraging ecology of the Galápagos Islands carpenter bee, *Xylocopa darwinii* (Linsley et al., 1966). Subsequent observations of this species have not reconfirmed the presence of nectar (McMullen, pers. comm. in Renner, this volume). During our own field investigations of this species, no suitable material could be located to resolve this question. An additional, as yet unidentified, *Miconia* species from lowland Amazonia has recently been reported to produce nectar (Roubik, pers. comm. in Renner, this volume).

MEMECYLACEAE

Memecylon and *Mouriri* have a peculiar depressed gland on the backside of the anther connective (Figs. 22, 24). This structure was early described as a nectary (Burck, 1891; Subramanyam, 1949; Venkatesh, 1955) but recently has been hypothesized to be an elaiophore, or oil-producing gland (Buchmann & Buchmann, 1981). Anatomical sections reveal this gland to be composed of more or less radially enlarged epidermal cells, which are clearly distinguishable from other cells of the connective (Figs. 23, 25).

Pternandra is variously included in or excluded from the Memecylaceae. Its uncertain status is based largely on the absence of the anther connective glands found in other members of Memecylaceae. The two species examined in this study, *P. caerulescens* Jack. and *P. echinata* Jack., lack these gland structures on the surface (Figs. 26, 27) and in section (Fig. 28).

Discussion

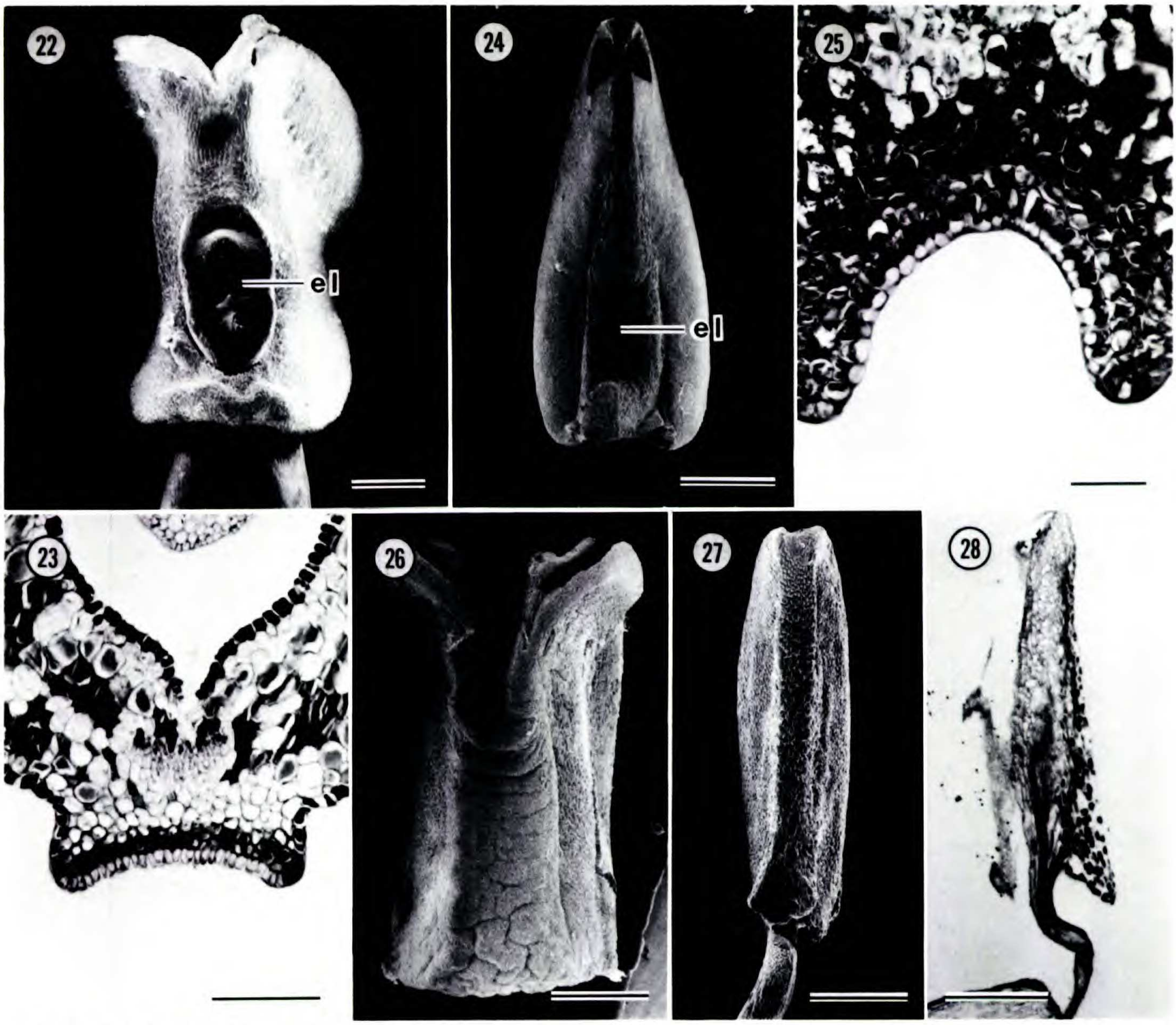
POSITION AND STRUCTURE OF FLORAL NECTARIES IN MELASTOMATACEAE

The present study shows that, in contrast to nearly all other myrtalean families, Melastomataceae lack histologically differentiated nectariferous tissue either on the inner surface of the floral tube, on the gynoecium, or at the floral tube–gynoecium junction. While nectar production in Melastomataceae is rare, a diversity of unusual nectary types are implicated, including secretion from the stamens, petals, and perhaps stigmas. Most documented nectar-producing melastomes secrete nectar from the stamens, although we did not find any differentiated nectariferous structures or tissue in that organ. On the basis of observations and anatomical structure, we thus conclude that in most nectariferous Melastomataceae nectar is produced by a nonstructural nectary consisting solely of the staminal vascular bundles.

Compared with melastome species generally, stamens of nectar-producers have a much thicker vascular bundle containing many small, densely staining cytoplasm-rich phloem cells. An ultrastructural survey of these cells could offer additional evidence of their nectar-secreting capability, since there is a clear connection between cytological constituents and processes of nectar secretion (for review of ultrastructural features see Fahn, 1979).

The nonlocalized nature of these androecial nectaries may help resolve the conflicting reports about the specific sites of nectar secretion (Table 2). If nectar is produced by the staminal vascular bundle, it could emanate from almost anywhere along the stamen. Additionally, if the direction of the nectar stream within a stamen is affected by gravity, the secretion site could differ between stamens and among individual flowers.

Several observers, including one of us (B.A.S.), have noticed that in certain genera (e.g., *Brachyotum* and *Tibouchina*) the location of nectar secretion appears to be closely associated with a small slit in the adaxial surface of the filament (see arrows in Figs. 1–3, 6). The development and significance of these slits is somewhat controversial. We found no anatomical differentiation of this structure. Since stamens in Melastomataceae are folded or bent inward in bud, becoming more or less straight at anthesis, the observed slitlike structures may form spontaneously and be unrelated to nectar secretion.



FIGURES 22–28. *Memecylon*, *Mouriri*, and *Pternandra*.—22, 24. Scanning electron micrographs (SEM) of anthers of *Memecylon caeruleum* and *Mouriri nervosa*, showing anther glands on backside of connective.—23, 25. Transverse sections of anther glands of *Memecylon caeruleum* and *Mouriri nervosa*.—26, 27. SEMs of anthers of *Pternandra echinata* and *P. caerulescens*, showing absence of glands on backside of connective.—28. Longitudinal section of stamen of *Pternandra caerulescens*. Abbreviation: el, anther elaiophore. Scale bars = 0.5 mm in Figures 24, 26, 27, and 28; 0.2 mm in Figures 22, 23; 0.05 mm in Figure 25.

Such slits are, in fact, reported in some species not known to secrete nectar (Renner, this volume). However, an apparent association of these slits with nectar-producing species, their absence in related non-nectariferous species (e.g., *Blakea chlorantha* vs. *B.* sp. nov. and *B. foliacea*), and field observations of nectar droplets formed precisely at these indentations strongly argue for a role in nectar secretion. These structures may form through a deterioration of a small amount of tissue on the inner side of the geniculum, providing an exit pathway for nectar produced by the staminal vascular bundle. Clearly, a systematic survey of the occurrence of these slits throughout the Melastomataceae would be useful in clarifying their role.

Although nectar production has been reported in *Miconia minutiflora* (Mori & Pipoly, 1984; Mori, pers. comm., 1986), Renner (this volume) has questioned whether the fluid observed was truly nectar. From our anatomical examination, *Miconia minutiflora* does not appear capable of secreting nectar from the stamens in the manner of the other confirmed nectar-producers we investigated. If nectar production in this species is reconfirmed, the conspicuous stigma, which is subtended by cytoplasm-rich vascular tissue, should be closely examined for a possible secretory role. Stigmatic nectar secretion is rare within the angiosperms but occurs in Asclepiadaceae and Araceae (Fahn, 1979).

EVOLUTION OF FLORAL NECTARIES IN MELASTOMATACEAE

Nectaries generally consist of an epidermis subtended by specialized parenchyma cells (Esau, 1977;

Fahn, 1979). The phloem-based nectaries we have found in Melastomataceae, which have no structurally differentiated parenchyma, are a rather extreme deviation from this typical structure. The nonstructural androecial nectaries found in Melastomataceae are particularly anomalous in Myrtales, where, of the 14 families currently included in the order (Dahlgren & Thorne, 1984), only Melastomataceae, Memecylaceae, and Rhynchocalycaceae lack densely staining structural nectaries. Eyde (1981) has discussed evolutionary shifts in the location of floral nectaries in flowers of various myrtalean families and concluded that the ancestral site of nectar secretion for Myrtales, as for many other dicots, is the junction between the gynoecium and the floral tube or, in tubeless flowers, the junction with the androecium. From this ancestral position, nectaries evolutionarily have migrated onto the floral tube, or even onto the androecium in some tubeless species of *Lopezia* and *Epilobium* of the Onagraceae (Eyde & Morgan, 1973; Eyde, 1981). Androecial nectaries are also found in other groups, including virtually all members of the Caryophyllales (Zandonella, 1977). However, the androecial nectaries in these other families are more typical differentiated structures and thus not comparable to the nonstructural androecial nectaries of Melastomataceae, which are certainly unique within the Myrtales and perhaps among angiosperms as a whole.

Given the ancestral myrtalean nectary type and position proposed by Eyde (1981), it seems clear that structural nectaries were lost in the evolutionary lineage ancestral to Melastomataceae and Memecylaceae. Such nectaries appear to have been lost independently in the lineage leading to Rhynchocalycaceae (a monotypic family consisting only of the South African *Rhynchocalyx lawsonioides* Oliver), since on many other grounds this family is more closely related to other members of the Myrtales than to Melastomataceae (Tobe & Raven, 1984).

Pollinator interactions appear to have played a key role in both the ancestral loss and subsequent re-evolution of nectaries within the Melastomataceae. Melastomataceae are, on the whole, a family uniquely suited for bee pollination. The distinctive poricidally dehiscent anthers are directly related to vibratile extraction of pollen by bees, a phenomenon known as buzz pollination. Bees foraging for pollen in this manner rarely forage simultaneously for nectar, and then only to mix it with the pollen to improve the pollen's handling properties (Buchmann, 1983). Although poricidal anthers are found in numerous angiosperms (for review see Buchmann, 1983), few plant families are so completely characterized by this feature as Melastomataceae. Given the widespread distribution of poricidal anthers within all lineages of Melastomataceae, this feature appears to be the ancestral condition for the family. Thus, if buzz pollination became established in the lineage ancestral to Melastomataceae, there would be little or no selective advantage in maintaining energy-expensive nectaries. By attracting undesirable and potentially destructive floral visitors, nectaries may even have been selected against in protomelastomes.

Nectaries appear to have re-evolved independently in several distinct lineages within the family, most of which share certain ecological and reproductive traits. Cruden (1972) has pointed out the potential reproductive advantage ensuing from a shift from bee to bird pollination in wet-tropical montane ecosystems. Similarly, Heinrich & Raven (1972) have noted the increased energy reward necessary to attract pollinators operating at higher elevations and to support vertebrate rather than invertebrate pollinators. Nectar, composed principally of carbohydrates, is a much richer energy source than pollen and is almost invariably the floral reward used to attract vertebrate pollinators. Not surprisingly, most confirmed nectar-producing Melastomataceae (species of *Blakea*, *Brachyotum*, *Chalybea*, *Huilaea*, and *Tibouchina*) occur at high or relatively high elevations, and are known or presumed to be pollinated by vertebrates (Table 2).

According to traditional and recent classification systems for the family (Cogniaux, 1891; van Vliet et al., 1981; Wurdack, 1980), confirmed nectar-producing Melastomataceae are found in at least four different tribes: Blakeae, Dissochaeteae, Miconieae, and Tibouchineae (see Table 1). The phylogenetic relationships among these tribes are not yet resolved, but they undoubtedly do not form a monophyletic lineage within the family. In addition, the majority of genera in these four tribes are not known to produce nectar. Except for the lowland species of *Miconia* discussed above, most of the nectar-producing taxa can be viewed as relatively derived within their respective tribes in terms of pollination systems and ecological/altitudinal preferences. With regard to the latter, the Central and northwestern South American montane terrains that are inhabited by many of these species (and, if the above interpretation is correct, may have provided the ecological impetus for the development of nectar rewards) are generally more recent (Zeil, 1979)

than the origin of the Melastomataceae, fossils of which are known from as early as Eocene times (Hickey, 1977).

Two hypotheses can be advanced to account for the unusual systematic distribution of nectaries within the family. The first is that such nectaries are the basal condition in Melastomataceae and have been lost in the vast majority of species. Given the structural nectaries present in other families of Myrtales and the rather specialized morphological state of most of the nectariferous species, however, such an interpretation is untenable. Renner (this volume) advocates a modified version of this hypothesis, suggesting that "the capacity for developing nectaries is basic in the Melastomataceae but suppressed in most modern members." This supposition seems equally difficult to accept. Rather, we propose a second hypothesis, which is that nectaries have evolved independently a number of times within the family and developmentally have followed the easiest course available. Two lines of evidence point to this. First, three different nectary types have developed within the family, each involving different floral organs (stamens, pistil, petals). Although rare within angiosperms, the most common melastome nectaries, nonstructural androecial nectaries, involve very little modification of existing structures and thus appear to be an easily developed solution to producing nectar. It is difficult, however, to reconcile this view of the ease of developing such nectaries with the relative rarity of nonstructural androecial nectaries in the angiosperms as a whole.

SYSTEMATIC IMPLICATIONS OF NECTARY ANATOMY FOR MEMECYLACEAE

Memecylaceae traditionally have been included in Melastomataceae as a tribe or subfamily (e.g., Cogniaux, 1891; Morley, 1976). Based on floral nectary characters, Memecylaceae agree with Melastomataceae in completely lacking densely staining structural nectaries. The term "disc" has sometimes been used to describe certain structures within the flowers of *Memecylon* (see Bremer, 1983). Given the complete lack of nectariferous tissue, this term should, however, be avoided. As previously discussed, loss of structural nectaries seems to be a feature ancestral for Melastomataceae, and this is probably also the case for Memecylaceae. We regard loss of structural nectaries as a synapomorphy uniting these two families.

Memecylaceae have generally been circumscribed to include the Old World *Memecylon* and the New World *Mouriri* and *Votomita*, all containing anther connective glands. Based on observations of *Mouriri myrtilloides* (Sw.) Poir, Buchmann & Buchmann (1981) suggested that the connective glands of *Memecylaceae* are elaiophores that secrete lipids for nutritional use by pollinating bees, primarily in larval provisioning. Although the secretion is lipid rich, its chemical complexity and the presence of components seemingly toxic to insects have led others to be cautious about this interpretation (Renner, this volume; Simpson & Neff, 1981).

Morley (1976) considered these distinctive but little-understood connective glands to be one of the most characteristic features of the "Memecyleae" (= Memecylaceae), even though they are occasionally lost, as in *Mouriri exadenia* Morley. Whatever its taxonomic rank, the group is now generally considered to include additional genera, among them *Pternandra*, which lacks connective glands (Dahlgren & Thorne, 1984). The present study reconfirms this observation: all examined species of *Memecylon* and *Mouriri* have anther glands on the backside of the connective, whereas all examined species of *Pternandra* lack them. Therefore, even if *Pternandra* is aligned with *Memecylon*, *Mouriri*, and *Votomita* at the familial level, evolution of the anther glands appears restricted to the lineage including the three last-mentioned genera. Available evidence from staminal anatomy does not resolve the correct familial placement of *Pternandra* but does suggest that if included in Memecylaceae, it should be regarded as the sister group to the rest of the family. This is generally the approach taken by van Vliet et al. (1981) in placing *Pternandra* in its own tribe Pternandreae of their "Memecyloideae" (= Memecylaceae).

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